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## REPORT

# Long-term fitness benefits of egg sex modification by the Seychelles warbler

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## Abstract

Sex-ratio theory states that if the fitness costs to the parents of producing one offspring's sex relative to the other are higher, parents should discount these costs by producing fewer individuals of the more costly sex. In the co-operatively breeding Seychelles warbler (*Acrocephalus sechellensis*) mothers adaptively modify the sex of their single egg toward daughters, the helping sex, when living on territories with rich resources where helpers increase parental reproductive success, but toward sons, the dispersing sex, when living on territories where resources are scarce and/or no helping benefits accrue. By modifying offspring sex ratio, parents maximize their inclusive fitness benefits. Pairs in high-quality territories gained significantly more inclusive fitness benefits (through helping and reproducing offspring) from the production of daughters than from sons, and vice versa in low-quality territories (through reproducing offspring). Experimental manipulation of the offspring's sex shows that the consequences of sex allocation are adaptive for parents on high-quality territories. On high-quality territories with female production, breeding pairs raising step-daughters gained significantly higher inclusive benefits (through indirect and direct fitness gains) than by raising step-sons.

## Keywords

Egg sex modification, experimental sex manipulation, long-term benefits, sex ratio theory, Seychelles warbler.

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## INTRODUCTION

According to sex-ratio theory, when parents decide on the sex ratio of their progeny, they should take into account how their decision affects their own future reproductive prospects and thus how it affects the reproductive prospects of their offspring (Trivers & Willard 1973; Frank 1990). If ecological or social factors increase the fitness costs to the parents of one sex relative to the other, parents should discount these costs by producing fewer individuals of the more costly sex (Trivers & Willard 1973). In 1982, Charnov stated that nothing much of interest was going on with regard to progeny sex ratios in birds, because of meiotic constraints and the difficulties of sexing young birds (Charnov 1982). Avian mothers are the heterogametic sex and hence the offspring's sex is determined by sex chromosomes from the female parent. With the development of new molecular tools for genetic sexing in birds (Griffiths *et al.* 1996; Lessells & Mateman 1996), however, several avian studies have shown that chromosomal sex determination may not prevent birds

from adaptive adjustment of egg sex ratios. Individual females can facultatively control the sex of offspring they produce, and in some cases it is shown that females increase their future reproductive success by adaptively modifying the primary sex ratio (Komdeur *et al.* 1997; Sheldon *et al.* 1997). However, it is unknown whether individual parents gain benefits of sex manipulation through increased reproductive success of their offspring. For the long-term adaptive nature of sex manipulation it is crucial to know whether the positive effect on the reproductive success of breeding pairs is counterbalanced by the negative effect on reproductive success for sons and daughters. Evidence for the long-term adaptive nature of sex ratio variation has been presented only for the kestrel (*Falco tinnunculus*) and the collared flycatcher (*Ficedula albicollis*). In the kestrel, the seasonal decrease in the proportion of male offspring is adaptive because of the seasonal decline in the probability that males (but not females) breed at 1 year of age (Dijkstra *et al.* 1990). In the flycatcher, forehead patch size of fathers is positively related with fitness of sons (Sheldon & Ellegren 1996).

Females paired with males with large forehead patches produce significantly more sons (Sheldon *et al.* 1997). So far the benefits of sex modification have never been measured following experimental manipulation of the offspring's sex. In this paper I will discuss the long-term fitness consequences of sex modification by comparing the fitness of male and female offspring in the Seychelles warbler (*Acrocephalus sechellensis*) in different situations.

Until 1988, the world population of the endemic Seychelles warbler was entirely confined to Cousin Island (29 ha), where it has reached carrying capacity of approximately 320 birds (Komdeur 1992). The warbler is insectivorous, gleaning insect food from leaves, usually has a one-egg clutch once per year, and has high annual adult survival (81.1%, 334 bird-years). The breeding pair remains in the same territory, sometimes for as long as 9 years. Both territory quality, measured in terms of insect prey density, and the presence of helpers are important factors affecting the fitness of parents. Although warblers can breed successfully at 1 year of age, daughters often delay reproduction and function as helpers at the nest, providing nourishment to their parents' offspring. Sons typically disperse. Seychelles warbler mothers adaptively modify the sex of their single egg toward the helping sex when living on territories with rich resources where helpers increase parental reproductive success, but toward the dispersing sex when living on territories where resources are scarce and/or no helping benefit accrue (Komdeur *et al.* 1997). The observed sex ratio variation supports both the "production-of-helpers" hypothesis (Emlen *et al.* 1986; Lessells & Avery 1987) as well as the local resource competition hypothesis (Clark 1978). In the short term, the manipulation of the offspring's sex is directly adaptive from the perspective of the breeding pair, but how it affects the reproductive success of the breeding pair in the long term has not been tabulated before. I investigate the long-term fitness benefits of egg sex manipulation by comparing lifetime reproductive success of offspring of each sex produced on low- and high-quality territories using 13 years of detailed life-history data from an individually marked and genealogically known population. In addition, I show the adaptiveness of egg sex-ratio modification by experimental manipulations of the offspring's sex ratio.

## MATERIALS AND METHODS

### Data collection

On Cousin, all 115–123 breeding territories (310–400 birds) were checked regularly (every 2 weeks during 1985–91; every 4 weeks during 1992–97) for young and the presence of colour-ringed birds from December 1985

to August 1997. Data were based on individually colour-ringed birds. As warblers rarely colonize other islands by themselves [out of 2156 ringed adults, only one bird (0.05%) is known to have flown from Cousin Island to Cousine Island], I assumed that missing birds had died if they were not found on other territories. In 1985–97, most nestlings were colour ringed, and in 1993–95 all nestlings between 4 and 12 days old produced by unhelped breeding pairs and adults were blood sampled for sexing using RAPD markers (Komdeur *et al.* 1997).

Territory quality was expressed as mean insect prey available within a territory, because adult survival and reproductive success correlated positively with this. Territory quality was measured each month (for method, see Komdeur 1992), and the average yearly territory quality was divided into three classes: low (0–1500 insects present), medium (1,501–3000 insects), and high (> 3000 insects). Over the period 1985–97 the quality of territories has remained stable (see also Komdeur 1996a). In 1986 and 1987 all warbler territories on Cousin Island were checked fortnightly for the occurrence of male and female breeding vacancies for yearlings to fill. Warbler breeding vacancies for either male or female arise on existing territories through the death of the dominant male or female bird in that territory (Komdeur 1991).

### Definitions of variables

*Age:* age (years) of the bird, based upon known hatching dates.

*Focal breeding pair:* unhelped breeding pair producing offspring in 1985 and 1986 that survived to at least 6 months of age.

*First-generation offspring:* male and female offspring that survived to at least 6 months of age, which were produced by focal pairs in 1985 and 1986.

### Fitness accounting

Warblers can be correctly sexed at 6 months of age and older by biometrics (Komdeur 1991). The sex ratio of hatchlings produced by unhelped breeding pairs that were sexed between 4 and 12 days old in 1993–95 (Komdeur *et al.* 1997) and the sex ratio of these hatchlings surviving to 6 months of age, were both male biased on low-quality territories, at parity in medium-quality territories, and female biased on high-quality territories (Table 1). As sex ratios of hatchlings and 6-month-old birds per territory class were similar (Table 1), I assume that the observed offspring sex ratio at 6 months of age typically reflects the egg sex ratio at laying. To determine the fitness consequences of sex modification, I estimated the inclusive fitness consequences of producing sons and

**Table 1** Sex ratio of Seychelles warbler nestlings and sex ratio of these nestlings surviving 6 months of age (1993–95), and sex ratio in 6 month old warblers and number of sons and daughters reaching 1 year of age produced by unhelped warbler pairs in relation to quality class of breeding territory (1985–86), and number of breeding vacancies present for these yearlings on different quality territories (1986–87).

Tq class	Sex ratio (1993–95)			Sex ratio (1985–86) 6-month-old young	No. 6-month-old young reaching 1 year of age		Breeding vacancies (1986–87)	
	nestlings	nestlings surviving 6 month of age	<i>P</i> *		Sons	Daughters	Males	Females
Low	77.2 (57)	70.8 (24)	0.547	75.0 (32)	18	5	10	6
Medium	55.2 (27)	46.7 (15)	0.454	60.0 (15)	9	6	5	4
High	12.5 (32)	13.8 (23)	0.953	28.6 (14)	4	10	1	1

In the analysis only young were included that had been hatched from different breeding pairs. Numbers of individuals are in parentheses. Percentage sons =  $100/(1 + e^{-z})$ ,  $z = 2.14-0.97$  (tq class), *G*-test of independence:  $D = 8.60$ , d.f. = 1,  $P = 0.0034$ ,  $n = 61$  (tq classes: 1, low-quality territory; 2, medium-quality territory; and 3, high-quality territory)

\**P* values for differences between sex ratio of nestlings and sex ratio of these nestlings surviving 6 months of age (1993–95) were determined by  $\chi^2$  test.

daughters. During the period 1985–86, six unhelped pairs produced two nests with one young in each that survived the first 6 months of age. To avoid pseudoreplications only the first produced young was included in the analyses. On four occasions the breeding birds of a focal breeding pair that had produced a 6-month-old young in 1985–86 split up to form new pairs. However, none of these new pairs produced 6-month-old young during the period 1985–86. Of all the first-generation offspring, the dispersal tactics and reproduction have been recorded throughout their lives, and all died before the end of the study period. This enabled me to calculate a part of the inclusive fitness benefits of sex modification from the point of view of the focal breeding pair. Because 1 year is the minimum age at which warblers are capable of producing their first young, I calculated the partial inclusive fitness benefit of the focal breeding pair as the fitness through a first-generation son or daughter, which is the number of yearlings produced over a lifetime by son or by daughter. The fitness through a first-generation offspring ( $V$ ) is calculated as:

$$V = V_b + V_h \quad (1)$$

where  $V_b$  = (extra offspring through help by first-generation birds)  $\times$  (mother's relatedness to those offspring), and  $V_h$  = (first-generation bird's own offspring)  $\times$  (mother's relatedness to those offspring).

Helping first-generation offspring could affect the reproductive success of the focal breeding pair. The production of additional, related individuals beyond what the focal breeding pair might have produced, adds an indirect component to lifetime reproductive success (e.g. Emlen 1984; Grafen 1984; Koenig & Mumme 1987; Stacey & Ligon 1987). The estimated additional number of extra yearlings produced by the focal breeding pair

through help of their first-generation offspring of age  $i$  ( $V_{hi}$ ) is

$$V_{hi} = (V_{ni} - V)/h \quad (2)$$

with  $V_{ni}$  is the number of yearlings produced by the focal breeding pair with helper(s) in year  $i$ ,  $V$  is the mean number of yearlings produced by the breeding pair without helper(s) in other years, and  $h$  is the number of helpers assisting the breeding pair in that year. In some cases the value of  $V_{hi}$  is negative due to a decrease in production through resource competition (Komdeur 1992).

The indirect fitness obtained through helping first-generation offspring is given by:

$$V_h = \sum_{i=1}^{a-1} V_{hi} R_{m,hi} \quad (3)$$

where  $R_{m,hi}$  is the coefficient of relatedness between the mother and her first-generation offspring ( $R_{m,hi} \approx 0.5$ ), and  $a$  is the age of the first-generation offspring of first independent reproduction as a breeder. Apart from indirect effects through helping, the offspring's sex has no effect on survival of the focal breeding pair (Komdeur 1991).

The fitness obtained through direct reproduction of the first-generation offspring is given by:

$$V_b = \sum_{j=a}^w V_{bj} R_{m,bj} \quad (4)$$

$V_{bj}$  is the number of offspring produced by the first-generation offspring at age  $j$  (grand offspring of the focal breeding pair), and  $R_{m,bj}$  is the coefficient of relatedness between the mother and her first-generation's offspring (her grand offspring,  $R_{m,bj} \approx 0.25$ ). All but four breeding

pairs, which included a first-generation offspring, produced single young in a single nest. Four breeding pairs with a first-generation offspring and a “helping” grand daughter produced two chicks in a single nest. Because DNA fingerprinting showed that twins (i.e. two-egg clutches) produced on territories with female helpers are actually single young both sired by the breeding father, but one produced by the mother and one by their “helping” daughters (Kappe 1998), I estimated the average relatedness between the focal breeding pair and these twins [its grand offspring ( $R_{m,bj} \approx 0.25$ ) and grand grand offspring ( $R_{m,bj} \approx 0.125$ )] at 0.375.

### Experimental manipulation of offspring sex ratio

The sex-specific fitness consequences of sex allocation for male and female offspring was determined experimentally through swaps of 4–7-day-old nestlings of the “majority” and the “minority” sex between nests from unhelped breeding pairs. Only pairs of which both breeding birds were between 3 and 7 years old were included in the experiment, because between these ages there are no age-related changes in the average number of independent young produced per hatched egg (Komdeur 1996b). Because the “adaptive” nestling sex on high-quality territory (hiqt) is female and on low-quality territory (loqt) male (Komdeur 1992), I tried to generate two experimental groups and two control groups in 1994: pairs on hiqt who had produced a daughter receiving either a step-son (experiment) or a step-daughter (control), and pairs on loqt who had produced a son receiving either a step-daughter (experiment) or a step-son (control). Because the sex of the swapped nestlings was not known at the time of the swaps, the experimental and control groups were achieved by swapping nestlings between high-quality territories (three pairs), between a high-and a low-quality territory (six pairs), and between low-quality territories (three pairs) (Fig. 1), with the expectation that nestlings from high-quality territories were female and nestlings from low-quality territories were male (Komdeur 1991; Komdeur *et al.* 1997). All nestlings were blood sampled

and sexed at a later stage in the laboratory. Of the pairs on hiqt who had produced a daughter, five pairs received a step-daughter and five pairs a step-son. Of the pairs on loqt who had produced a son, four received a step-daughter and seven a step-son (Fig. 1). Only one pair on hiqt and one pair on loqt were excluded from the analyses because the original chick was of the “wrong” sex (Fig. 1). The maximal age difference between the swapped chicks was 2 days. The body condition (weight/ $\sqrt{\text{tarsus}}$ ) of pairwise swapped nestlings was the same ( $2.08 \pm 0.72$  vs.  $2.90 \pm 0.44$ ; paired-sample  $t$  test:  $t = 0.35$ , d.f. = 11,  $P = 0.730$ ). Warblers readily accept nestlings and they provision the nestling at the same rate as their own nestling (mean food provision rate/hour:  $17.75 \pm 3.96$  vs.  $19.17 \pm 4.37$ ; paired-sample  $t$  test:  $t = 1.35$ , d.f. = 11,  $P = 0.204$ ). For step-offspring the number of fledglings produced, either indirectly through helping or directly through breeding, during 1994–97 is known, which enabled me to estimate the partial inclusive fitness benefit (expressed in terms of fledglings) of the step-parents as the fitness accrued through a step-son or step-daughter.

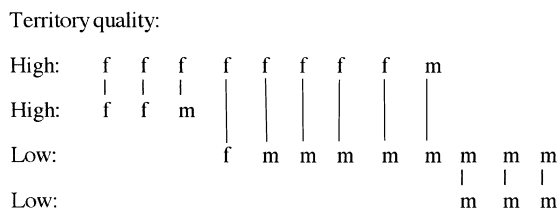
### Statistical analyses

The effect of territory quality on offspring sex ratio was analysed by logistic regression, and the effect of territory quality on LRS of different sex offspring by ANOVA analysis. Means are expressed with standard deviations, probability values are two-tailed, and the null hypothesis was rejected at  $P < 0.05$ .

## RESULTS

### Offspring sex modification and inclusive fitness

In 1985–86, the fraction of 6-month-old young males produced by unhelped breeding pairs changed significantly with territory quality (Table 1). Most young in low-quality territories were males. Neither sex predominated significantly in medium-quality territories, and young in high-quality territories were mainly females. These sex ratio values are similar to the sex ratio values of hatchlings and hatchlings reaching 6 months of age in 1993–95 (Table 1). Because reproductive success and survival of both sexes were higher in high-quality territories (Komdeur 1992), fewer breeding vacancies arose on high-quality territories through the death of a dominant breeding bird of the same sex (Table 1). On low-quality habitat more male yearlings were produced than there were breeding vacancies, whereas the production of female yearlings was in line with the number of breeding vacancies. Of these yearlings, seven males and four females filled low-quality breeding vacancies, four males



**Figure 1** Experimental design of nestling swaps between high- and low-quality territories in 1994 (|, swap). Sex of nestlings was determined using RAPD marker (f, female; m, male).

filled medium-quality vacancies, seven males became floaters without permanent residence, and one female became a helper on her natal territory. On medium-quality habitat, the production of male and female yearlings was a little higher than the number of male and female breeding vacancies, and of the yearlings produced all filled medium-quality breeding vacancies, but one male died soon after his first breeding attempt. On high-quality habitat more male and female yearlings were produced than there were breeding vacancies. All males dispersed and established small territories inserted between existing high- and medium-quality territories where they acquired a partner but failed to produce offspring. However, all these males eventually filled a breeding vacancy of high- or medium-quality territory, one female filled a high-quality vacancy at 1 year of age, nine females became helpers on their natal territory, of which five eventually filled a medium-quality breeding vacancy and four a high-quality breeding vacancy.

The indirect fitness benefits through helping first-generation offspring ( $V_h$ ), the fitness benefits through reproducing first-generation offspring (direct fitness,  $V_b$ ), and inclusive fitness benefits ( $V$ ) accrued to focal breeding pairs by producing sons or daughters on different quality territories are presented in Table 2. None of the focal breeding pairs in any quality territory gained indirect fitness through their male offspring and focal breeding pairs on low-quality territories did not gain indirect fitness benefits through their female offspring. Focal breeding pairs on medium- and high-quality territories gained significantly more indirect fitness benefits by producing daughters than by producing sons (Table 2). Focal breeding pairs on low-quality territories gained significantly more direct fitness benefits by producing sons than by producing daughters. For focal pairs on medium-quality territories the direct fitness benefits were equal for producing sons or daughters, and on high-quality territories the direct benefits gained from producing daughters were almost significantly higher than those gained from producing sons (Table 2). The inclusive fitness benefit was positively correlated with territory quality (ANOVA:  $F_{2,58} = 31.94$ ,  $P < 0.001$ ; Table 2). On low-quality territories pairs producing sons had 4.0 times higher inclusive fitness than pairs producing daughters. On medium-quality territories the inclusive fitness of pairs producing sons or daughters was similar, and on high-quality territories pairs producing daughters had 2.9 times higher inclusive fitness than pairs producing sons (Table 2). Standardized for the relative proportion of each type of territory, the average fitness gained from breeding independently was equal for sons and daughters [average yearlings produced by sons:  $2.23 \pm 1.20$  ( $n = 31$ ); average yearlings produced by daughters:  $3.81 \pm 3.11$  ( $n = 21$ ); Mann–Whitney  $U$  test:  $Z = 1.44$ ,  $P = 0.149$ ].

**Table 2** The indirect fitness benefits through helping first-generation offspring ( $V_h$ ), the fitness benefits through reproducing first-generation offspring (direct fitness,  $V_b$ ), and inclusive fitness benefits ( $V$ ) accrued to focal breeding pairs by producing sons or daughters (1985–1986) on different quality territories (see also Table 1)

Territory class:	Low			Medium			High		
	Sons	Daughters	$P^*$	Sons	Daughters	$P^*$	Sons	Daughters	$P^*$
First generation:									
Total helping lifespan (years)	$0.12 \pm 0.34$	$0.25 \pm 0.71$	0.949	$0.00 \pm 0.00$	$1.50 \pm 0.84$	0.005	$0.00 \pm 0.00$	$3.30 \pm 1.64$	0.008
Mean indirect yearlings produced/year ( $V_h R_{m,i}$ )	$0.00 \pm 0.00$	$-0.01 \pm 0.04$	0.623	–	$0.32 \pm 0.19$	–	–	$0.41 \pm 0.27$	–
Fitness through helping offspring ( $V_h$ )	$0.00 \pm 0.00$	$-0.03 \pm 0.07$	0.623	$0.00 \pm 0.00$	$0.60 \pm 0.42$	0.005	$0.00 \pm 0.00$	$1.63 \pm 1.22$	0.024
Breeding life span (years)	$1.79 \pm 2.63$	$1.38 \pm 1.30$	0.078	$2.89 \pm 1.17$	$3.00 \pm 2.09$	0.689	$6.75 \pm 0.96$	$4.70 \pm 1.83$	0.076
Mean yearlings through offspring/year ( $V_b R_{m,i}$ )	$0.21 \pm 0.17$	$0.08 \pm 0.12$	0.078	$0.43 \pm 0.14$	$0.34 \pm 0.14$	0.272	$0.34 \pm 0.14$	$0.68 \pm 0.21$	0.008
Fitness through breeding offspring ( $V_b$ )	$0.73 \pm 0.68$	$0.19 \pm 0.26$	0.029	$1.17 \pm 0.43$	$0.83 \pm 0.26$	0.181	$1.63 \pm 0.75$	$3.15 \pm 1.29$	0.054
Inclusive fitness ( $V$ )	$0.75 \pm 0.68$	$0.19 \pm 0.26$	0.026	$1.17 \pm 0.43$	$1.43 \pm 0.40$	0.181	$1.63 \pm 0.75$	$4.78 \pm 2.36$	0.014
$n$	24	8		9	6		4	10	

\* $P$  values for differences between sons and daughters were determined by two-tailed Mann–Whitney  $U$  test.

## Experimental sex manipulation and reproductive success

All foster-young reached 6 months of age. The indirect fitness benefits through helping step-offspring ( $V_b$ ), the fitness benefits through reproducing step-offspring ( $V_b$ ), and inclusive fitness benefits ( $V$ ) accrued to foster breeding pairs by raising step-sons or step-daughters on different quality territories are presented in Table 3. Foster pairs on low-quality territory did not gain indirect fitness through their step-sons. Although the direct and inclusive fitness benefits of raising step-sons were higher than of raising step-daughters, the differences were not significant (Table 3). Of the step-sons, two died before reaching 1 year of age, three became floaters of which one eventually filled a low-quality breeding vacancy and one a medium-quality-breeding vacancy, and two filled low-quality breeding vacancies at 1 year of age. Of the step-daughters, two died before reaching 1 year, one became a helper for her foster parents, and one filled a low-quality breeding vacancy. Foster pairs on high-quality territory gained significantly more indirect and direct fitness benefits, and, hence, inclusive fitness benefits, by raising step-daughters than by raising step-sons (Table 3). Of the step-sons, three established small territories inserted between existing territories and only one acquired a partner, and one stayed as a non helper with his foster-parents and eventually filled a low-quality breeding vacancy. Of the step-daughters, four became helpers for their foster-parents and one filled a high-quality breeding vacancy.

## DISCUSSION

### Adaptive offspring sex ratio optimization

In the long term, warbler breeding pairs and their male and female offspring benefit from the adjustment of sex allocation strategies. (i) Pairs in high-quality territories gained significantly more inclusive fitness benefits from the production of daughters than from sons (through indirect and direct fitness gains), and vice versa in low-

quality territories (through direct fitness gains). However, when standardized for the relative proportion of each kind of territory, the average fitness gained from breeding independently was similar for sons and daughters. (ii) In my experiment, on high-quality territories step-daughters had higher reproductive success than step-sons, and vice versa on low-quality territories with male production. Apart from the Seychelles warbler, I know of no empirical and experimental demonstration in birds that the sex ratio manipulation actually results in an increased long-term inclusive fitness for the breeding pair. Although my data set is more complete than most, there is still an element of ambiguity. In the Seychelles warbler it is desirable to take into account extra-pair fertilizations in the calculations of the inclusive fitness consequences of sex allocation for both parents, and (step-)offspring. Preliminary RAPD analyses indicate that less than 20% of nestlings were sired by males from outside the breeding territory (Kappe 1998). Ideally, my estimates of inclusive fitness should include the reproductive success of all sons and daughters produced over their lifetime rather than in just one season. Since 1994, nearly the complete warbler population including all nestlings has been blood sampled before mortality, sexed, and genotyped, thus allowing precise determination of inclusive fitness consequences of sex allocation for parents and offspring (including the young that die at a very early stage).

On the basis of the Seychelles warbler data, I would expect converse primary sex ratio biases in co-operative breeders that exhibit the more usual pattern of female-biased dispersal and male philopatry. Evidence for this has been presented only for the red-cockaded woodpecker (*Picoides borealis*), the bell miner (*Manorina melanophrys*), and the African wild dog (*Lycaon pictus*). The bell miner has a primary male-biased sex ratio (59.6%,  $N = 213$ ; Binomial test,  $P = 0.006$ ; Painter & Clarke, personal communication) and the red-cockaded woodpecker a secondary male-biased sex ratio (Gowaty & Lennartz 1985), and a possible explanation is that males of both species frequently assist their parents in rearing future young. Similarly, in African wild dogs, sons remain in

**Table 3** The indirect fitness benefits through helping step-offspring ( $V_b$ ), the fitness benefits through reproducing step-offspring (direct fitness,  $V_b$ ), and inclusive fitness benefits ( $V$ ) accrued to focal breeding pairs by raising step-sons or step-daughters (1994–98). In 1994, male nestlings produced on low-quality territories and female nestlings produced on high-quality territories by unhelped pairs were swapped for nestlings of different sexes (see also Fig. 1). Fitness benefits were expressed in terms of fledglings accrued to foster breeding pair

Territory class:	Low			High		
	Step-sons	Step-daughters	$P^*$	Step-sons	Step-daughters	$P^*$
Offspring:						
$V_b$	0.00 $\pm$ 0.00	-0.18 $\pm$ 0.56	0.527	0.00 $\pm$ 0.00	0.32 $\pm$ 0.19	0.032
$V_b$	0.86 $\pm$ 0.90	0.13 $\pm$ 0.25	0.230	0.10 $\pm$ 0.22	0.70 $\pm$ 0.27	0.016
$V$	0.86 $\pm$ 0.90	-0.05 $\pm$ 0.49	0.164	0.10 $\pm$ 0.22	1.02 $\pm$ 0.16	0.008
$n$	7	4		5	5	

\* $P$  values for differences between step-sons and step-daughters were determined by two-tailed Mann–Whitney  $U$  test.

their natal group and commonly help their mother to raise subsequent litters, and birth sex ratios are consistently male biased (Malcolm & Marten 1982). Primary sex ratios and the effects of sexual size dimorphism on energy costs of producing sons and daughters on offspring sex ratios have been studied in detail in raptors, where females are larger than males (Dijkstra *et al.* 1990; Daan *et al.* 1996), and in the red-winged blackbird (*Agelaius phoeniceus*), where males are the larger sex (Fiala 1981). The long-term fitness benefits of sex modification should be examined in other passerine bird species with and without sexual size dimorphism. Simulation models should be developed that predict the decisions individuals should make in terms of which sex to produce under certain resource and demographic conditions.

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## BIOSKETCH

J. Komdeur's research interests include the understanding of sex allocation and the occurrence of extra-pair behaviour in bird species. In addition, he is interested in what mechanisms and factors may influence primary sex ratios in species with and without sexual size dimorphism, and in the fitness consequences of sex allocation for each parent.